

THE SONORAN SUBSPECIES OF THE LIZARD *CTENOSAURA HEMILOPHA*

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ABSTRACT.— Five subspecies of *Ctenosaura hemilopha* are recognized, including *C. h. hemilopha* from Baja California; *C. h. insulana* from Isla Cerralvo, Gulf of California; *C. h. conspicuosa* from Isla San Esteban and (?) Isla Lobos, Gulf of California; and two new subspecies: *C. h. macrolopha* from Sonora and northern Sinaloa, and *C. h. nolascensis* from Isla San Pedro Nolasco, Gulf of California. The species is thought to have evolved from *C. pectinata*, through the somewhat similar *C. h. macrolopha* or its forerunner. Its range probably extended at an earlier time northward around the Gulf of California, thence southward through Baja California, with populations reaching certain Gulf islands from the peninsula, not from mainland Mexico, despite greater proximity of some of the islands inhabited to Sonora than to the peninsula.

It has long been known that populations of *Ctenosaura hemilopha* (Cope) of Sonora and adjacent areas differ from those of Baja California (Smith, 1935: 140-141; Lowe and Norris, 1955: 90). The peninsular subspecies was identified as *C. h. interrupta* Bocourt, 1882, by Lowe and Norris (*loc. cit.*), the mainland subspecies as *C. h. hemilopha* (Cope), 1863. The type-locality of *Cyclura* (*Ctenosaura*) *hemilopha* Cope is, however, "Cape St. Lucas," Baja California, and therefore Bocourt's *Ctenosaura interrupta* (type-locality Baja California) is a junior synonym of it, as noted by Hardy and McDiarmid (1969: 122). Accordingly, the mainland subspecies is presently nameless. It is here named

Ctenosaura hemilopha macrolopha, subsp. nov.

HOLOTYPE.— Chicago Natural History Museum 108705 (formerly E. H. Taylor 235), La Posa, San Carlos Bay, 10 mi NW Guaymas, Sonora, 30 June 1934, E. H. Taylor coll. PARATYPES: Univ. Illinois Mus. Nat. Hist. 20232 (formerly E. H. Taylor 121), 5 mi SW Hermosillo, Sonora, 26 June 1934, E. H. Taylor; Univ. Colorado Mus. Nat. Hist. (UCMNH) 42536, Yepáchic, Chihuahua, 5800 ft, summer 1970, Campbell Pennington; Brigham Young Univ. 14616-24, Urique, Chihuahua.

DIAGNOSIS.— A mainland Mexican geographic segment of *C. hemilopha* with a long middorsal crest reaching to groin and usually with 8 or more whorls of enlarged caudal scales separated from adjacent such whorls by no more than a single intercalary row of scales at any point.

DESCRIPTION OF HOLOTYPE.— A mature male, 194 mm s-v; pattern as depicted in Smith (*op. cit.*: pl. 23) and measurements as given in the same work (*op. cit.*: 141).²

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²Art. 13 of the International Code of Zoological Nomenclature permits "a definite bibliographic reference" even to the required "statement that purports to give characters differentiating the taxon"—i.e., the "diagnosis" of a new name. Since that statement is given here, a bibliographic reference to the nomenclaturally less essential *description* is presumably acceptable.

COMPARISONS.— The species *C. hemilopha* differs trenchantly from *C. pectinata*, its nearest neighbor, by having the whorls of small scales between the whorls of enlarged scales reduced to less than two complete whorls (except on the middorsal line, where there is often one spine) over a large part of the tail, whereas on no part of the tail in *pectinata* are there fewer than two complete whorls of small scales (except at the middorsal line). In addition,



Fig. 1. Ranges of the subspecies of *Ctenosaura hemilopha* and of nearby populations of *C. pectinata*. The dots indicate localities of record. 1, *C. h. hemilopha*; 2, *C. h. conspicuosa* on Isla San Esteban; 2a, *C. h. conspicuosa* (?) on Isla Lobos; 3, *C. h. nolascensis* on Isla San Pedro Nolasco; 4, *C. h. insulana* on Isla Cerralvo; 5, *C. h. macrolopha*; P, *C. pectinata*. The projected range of *C. h. hemilopha* corresponds with the limits of the San Lucan herpetofaunal area as mapped by Savage (1960:194). Localities and ranges in Sinaloa were drawn largely from Hardy and McDiarmid (1969:231). The projected range in Sonora is based largely upon Nelson and Goldman (1926: fig. 13). Base map courtesy Roger Conant.

the middorsal crest in all forms of *hemilopha* extends no farther posteriorly than a point somewhat anterior to the level of the groin; whereas in *pectinata* the crest extends to the level of the sacrum, terminating anywhere from the level of its anterior border to the base of the tail. *C. hemilopha* is also brownish in adults and subadults; whereas *pectinata* exhibits grayish or greenish tones throughout life, developing black markings on a gray background in adults. These distinctions hold throughout the 20 *C. pectinata* examined from the states of Sinaloa, Nayarit, Michoacán, Morelos, and Oaxaca, and 28 *C. hemilopha* representing all subspecies.

The mainland examples of *hemilopha* differ from all other populations of that species in possessing the longest dorsal crest occurring in the species, extending posteriorly nearly to the level of the groin, not quite reaching the level of the sacrum (as in *pectinata*); in all other populations of *hemilopha*, the dorsal crest ends at a level no more than $4/5$ the distance from axilla to groin. In addition, the mainland population differs from all other subspecies of *hemilopha* except *insulana* and *hemilopha* in usually having no evidence whatever of a second whorl of small scales between at least 8 adjacent whorls of enlarged scales, in the central region of the tail. Two of 10 *macrolopha* examined for this character failed to meet this criterion, having one or no whorl-set at all completely reduced to one intercalary row. In the other eight, the incomplete second row begins at points varying from the 16th whorl-set to the 24th, and in three the second row is not evident in any distal whorl posterior to the basal 4 or 5 whorl-sets. Adults retain narrow light bars on the forelegs.

REMARKS.— The subspecific name *macrolopha* (Gr., long crest) refers to the exceptionally long crest, reaching to level of groin, in the mainland population, as contrasted with the short crest (presumably the implication of *hemilopha*, Gr., half crest), reaching only a little beyond midtrunk in other populations of the species. In this respect *macrolopha* is intermediate between *pectinata*, with a crest uninterrupted or narrowly interrupted at sacrum, and insular-peninsular *C. hemilopha*. *C. pectinata* extends northward as far as about parallel 25°N, north of Culiacán about 20 miles, where its range meets, blends with or overlaps that of *C. hemilopha* (Hardy and McDiarmid, 1969:119-124, 231, fig. 44). Possibly, although the trenchant differences do not suggest it, the two populations hitherto designated as the species *C. pectinata* and *C. hemilopha* intergrade in the Culiacán area; if not, a certain amount of interspecific introgression seemingly occurred prior to attainment of reproductive isolation, accounting for the *pectinata*-like long crest in the mainland populations of *hemilopha*. Further field work will be required for a definitive conclusion.

RANGE.— The subspecies *C. h. macrolopha* ranges from the vicinity of Hermosillo, Sonora, through the northern third of Sinaloa, and inland as far as extreme western Chihuahua (Batopilas, Urique, Yepáchic). Bogert and Oliver (1945:334) conjecture that *C. hemi-*

lopha may once have occurred well north of its present range limits, the peninsular and mainland ranges being continuous north of the Gulf of California. The hypothesis is perhaps strengthened by the long-unconfirmed record of the species from Nogales (Bailey, 1928:21, et. al.). If valid in the context at least of former distribution, the record is no doubt referable to *macrolopha*. It occurs on no island, so far as now known.

Contrary to comments by Smith (*op. cit.*) and Lowe and Norris (*op. cit.*), the population on Isla San Pedro Nolasco, Sonora (about 13 mi W of the coast near Guaymas), differs sharply from *C. h. macrolopha* in having a short middorsal crest and at least partial second rows of small scales between most whorls on the tail. The specimen figured by Bailey (1928: pl. 5) from that island has a short crest, contrary to Smith's (*op. cit.*) interpretation. The greatest similarity in scutellation is to *conspicuosus*, but the pattern of the San Pedro Nolasco population is distinctive. That population is here named

Ctenosaura hemilopha nolascoensis, subsp. nov.

HOLOTYPE.— Univ. Colo. Mus. Nat. Hist. No. 26391, a subadult male, taken on Isla San Pedro Nolasco, Sonora, 16 August 1964, by T. Paul Maslin et. al. PARATYPES: Thirteen, all topotypes: UCMNH Nos. 26388-90, 26392-4, 35174-7, and one unnumbered; Mus. Comp. Zool. 13178-9.

DIAGNOSIS.— A geographic segment of *C. hemilopha* restricted to Isla San Pedro Nolasco, with enlarged scales of middorsal crest extending posteriorly no farther than a level about two-thirds the distance from axilla to groin; with rare exception, all whorls of enlarged scales separated from adjacent whorls by at least a partial second row of small scales on ventral surface of tail; a second row at least partially represented on dorsal surface through anterior 3-12 whorls (seldom more than 6); a third row at least partially represented in 5-7, usually 6 whorls; ventral surfaces of subadults with scattered rounded dark spots about $\frac{1}{3}$ diameter of tympanum; arm all black, lacking light bars, in adults; hind leg reticulated with black above, bars scarcely evident, in adults.

DESCRIPTION OF HOLOTYPE.— Enlarged scales of dorsal crest extending posteriorly about $\frac{4}{7}$ distance from axilla to groin; at least one complete intercalary row of scales between each pair of adjacent whorls of enlarged scales; a second intercalary row extending across ventral surface between all whorls, and represented dorsally also in the basal 6 sets of whorls, and in the 18th and following sets; at least part of a 3rd intercalary row present in the basal 7 sets of whorls, 4 in the basal 5, 5 in the basal 3, 6 in the basal 2 (the first set of whorls is arbitrarily counted as the one following the anteriormost whorl containing scales at least twice as large as those immediately preceding it); femoral pores 6-7. Snout-vent 167 mm; tail complete except for the terminal regenerated 50 mm, unregenerated part 248 mm.

Color in preservative a brownish slate; body unicolor above except for numerous small rounded dark flecks (each covering 1-9 scales, on sides of body, dim or absent near median line), two broad brownish black crossbands (one on shoulder, one just posterior to axilla, joined laterally), and a small round blackish brown spot on middorsal line at rear of neck; a few faint light spots on a dorso-lateral line on neck; forelegs black above, with poorly defined, narrow, light crossbars; hind leg essentially dark reticulated on a lighter background, the reticulum evidencing the broad dark bars and intervening light bands (about $\frac{1}{3}$ as wide as dark bars) of juveniles; tail with broad dark rings, 4 to 5 times as wide as intervening light rings, beginning at about 15th set of whorls. Throat and chest to near level of axilla dusky, with scattered lighter brown dots; rest of chest progressively less dusky posteriorly, lighter midventrally; ground color still lighter on ventral surfaces of legs and base of tail; numerous, randomly scattered, rounded, dark brown spots on ventral surfaces of abdomen, hind legs and base of tail, especially prominent on legs, somewhat larger than those on sides of abdomen, in general about $\frac{1}{3}$ the lesser diameter of tympanum.

VARIATION.— Smaller individuals have light crossbars on the back, 7 between axilla and groin; the legs are more prominently barred, the dark spotting on the ventral surfaces more extensive (the spots often arranged in transverse rows on abdomen) and the chin and lips prominently dark-and-light barred. A large adult male (estimated 400 mm s-v) is solid black over the throat, chest, forelegs, axilla, and shoulders; chin, lips, sides, and dorsal surface of neck gray brown; black crossing dorsum in two bands on shoulder; rounded median black spot on nape prominent; abdomen, both dorsally and ventrally, a light gray brown, with numerous very small black flecks laterally; groin rather heavily pigmented, but ventral surface of thigh with extensive light areas; dorsal surface of thigh densely but not coarsely reticulated, very little evidence of barring; feet and shank reticulate but barred.

Ten of the 11 paratypes examined for characteristics of the caudal whorls and crest have at least part of a second intercalary row (ventrally) between all adjacent pairs of whorl-sets; the one exception, No. 35176, has one intercalary row only in the 13th whorl-set. Five to 7 (usually 6) basal whorl-sets have at least parts of at least 3 intercalary rows, 3-5 (usually 4) have at least 4 or parts thereof. Three to 12 basal whorl-sets have at least 2 rows of intercalary scales represented dorsally. The enlarged scales of the dorsal crest extend posteriorly from $\frac{4}{7}$ to $\frac{4}{5}$ the distance from axilla to groin, usually about $\frac{4}{7}$.

COMPARISONS.— *C. h. nolascentis* differs more conspicuously from its geographically nearest population, in Sonora (*C. h. macrolopha*), than from any other subspecies. In *macrolopha* the dorsal crest extends nearly to groin, exceeding the limit of $\frac{4}{5}$ the distance from axilla to groin that marks the greatest extent in *nolascentis* and other subspecies. In addition, at least 8 whorl-sets in *macrolopha*

possess no more than one intercalary row, whereas that figure in *nolascensis* exceeds no more than one.

C. h. nolascensis is less markedly distinct from the other geographically more remote subspecies. *C. h. insulana* is similar to *macrolopha* (but differs from *nolascensis*) in having a large number of whorl-sets with no more than one row of intercalary scales (14 in the single specimen examined); its limbs are more prominently banded, and light crossbars persist on the trunk throughout life. *C. h. conspicuosa* loses the light crossbars in the postthoracic region and on limbs in adults, but is similar to *nolascensis* in caudal scutellation; the two specimens examined have 4-5 basal whorl-sets with more than two at least partial intercalary rows, 2-3 basal whorl-sets with more than three, and 2-4 basal whorl-sets with more than two intercalary rows dorsally; but it is likely that no real differences in these characters exist in comparison with other subspecies. *C. h. hemilopha* (4 specimens examined) has much the same scutellation as *insulana* and retains the light crossbars on the postthoracic region and hind limbs; in both these characters, it differs from *nolascensis*.

Unfortunately, it has not been possible to examine the caudal scutellation of an adequate series of all taxa. We have examined sufficient material of *pectinata*, *h. macrolopha*, and *h. nolascensis* to be confident of reliability of the characters observed, but the other subspecies of *hemilopha* (*insulana*, *conspicuosa*, *hemilopha*) need further observation not practical at the present time. Additionally, fieldwork in the area of contact of *pectinata* and *h. macrolopha* will be required to establish conclusively the interrelationships of these taxa, although we remain confident that no genetic interchange now takes place there and that the taxa are of specific rank relative to each other.

PHYLOGENY

The evolution of *hemilopha* and its subspecies is of major interest. Because *macrolopha* is more like *pectinata* than is any other race of *hemilopha*, and is geographically adjacent, it seems reasonable to hypothesize that *hemilopha* is a derivative of *pectinata* or a *pectinata*-like ancestor and that *macrolopha* more closely resembles the ancestral form of *hemilopha* than does any other race of the species. Because of the trenchant difference between insular-peninsular races on the one hand and the mainland race on the other, the close geographic proximity of the former group to the mainland, and the relative uniformity of characteristics of the members of the insular-peninsular group, it seems unlikely that the species radiated across the Gulf of California to the Peninsula. A more likely probability is that the species extended northward at one time, and thence into the Peninsula, and subsequently became more restricted in range, separating two components, one on the Peninsula and one on the mainland. *C. h. macrolopha*, remaining with or reestablishing contact with *pectinata* or its ancestor, maintained or developed a character displacement that accentuated the basic difference in caudal

scutellation between the two species, although *macrolopha* retained an intermediate character-state in extent of the crest, or perhaps introgression was responsible for the intermediacy.

The peninsular population diverged in character while in isolation, accentuating the brevity of the dorsal crest. Its range became essentially relic in nature, restricted to the southern third of the peninsula, except as a few waif populations in a sweepstake pattern reached a number of the Gulf islands. In their isolation from contact with other forms of the genus, these residual populations lost to varying degrees part of the unique caudal scale pattern, approaching but not achieving the presumably ancestral condition of *pectinata*.

With taxonomic recognition given to five geographically isolated populations of *hemilopha*, virtually all that exist (Soulé and Sloan, 1966:140), it is unlikely that any other extant subspecies will require recognition in the future, except perhaps for the population on Isla Lobos recorded by Lowe and Norris (1955:95). That population, so close to Tiburón island (not the Isla Lobos S of Guaymas), may perpetuate the group that no doubt formerly occurred on the larger island but is now extinct, probably due to human predation. Whether the Tiburón-Lobos populations have diverged sufficiently from others to merit recognition remains to be seen (Soulé and Sloan, 1966:140, refer Lobos material to *h. conspicuosa*). In any event, their relation to the peninsular-insular group as opposed to the mainland group is of major interest.

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KEY TO THE CTENOSAURA OF NORTHWESTERN MEXICO

1. All whorl-sets of tail containing at least two complete intercalary rows of scales (except sometimes on mid-dorsal line); dorsal crest extending to, onto or through sacral region; general color tone green (in juvenile) to gray (adults) *pectinata*
- No more than 6 basal whorl-sets of tail containing two complete intercalary rows of scales (excluding mid-dorsal line); dorsal crest not reaching sacral region; general color tone green (very young) to brown (subadults, adults)—*hemilopha* 2

- 2(1). Dorsal crest extending posteriorly nearly to groin, posterior to a point about $\frac{4}{5}$ distance from axilla to groin; usually at least 8 central caudal whorl-sets with no evidence whatever of a second intercalary row of scales *h. macrolopha*
 Dorsal crest terminating posteriorly near a point usually about $\frac{2}{3}$ distance from axilla to groin, or anterior thereto; central caudal whorl-sets with a partial second intercalary row or not 3
- 3(2). At least 8 central caudal whorl-sets with no evidence whatever of a second intercalary row of scales; light bars on limbs and postthoracic trunk retained throughout life 4
 No more than 1 or 2 caudal whorl-sets with no evidence whatever of a second intercalary row of scales; pattern diverse 5
- 4(3). Dorsal crest terminating posteriorly near a point about $\frac{2}{3}$ distance from axilla to groin *h. hemilopha*
 Dorsal crest terminating about at midabdomen *h. insulana*
- 5(3). Juvenile and young adults only with round dark spots (about $\frac{1}{3}$ lesser diameter of tympanum) scattered over ventral surfaces of trunk, hind legs and base of tail, becoming small dark flecks in adults; dark and light markings on limbs not sharply contrasted *h. nolascensis*
 Rounded dark marks on ventral surfaces of juvenile retained at least on hind limbs throughout life; light and dark markings of hind limbs sharply contrasted both above and below *h. conspicuosa*

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